

NATURAL HISTORY MISCELLANEA

Published by
The Chicago Academy of Sciences

Lincoln Park - 2001 N. Clark St., Chicago 14, Illinois

No. 70

October 23, 1950

The Distribution of the Races of *Desmognathus fuscus* in the Southern States

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The genus *Desmognathus* is widespread throughout the eastern United States and one species, *fuscus*, is divided into three races: the typical one, *brimleyorum*, and *auriculatus*. (The present paper will not include an evaluation of recently described forms: *ocoe* Nichols, *aeneus* Brown and Bishop, and *chermocki* Bishop and Valentine, or the exclusively montane desmognathus. None of these, apparently, belong to the species *fuscus*.) The distributional problems to be discussed center in the southern states; the ranges of the races north of Tennessee and North Carolina will not be considered here.

The accompanying pair of maps (Fig. 1) compares the distribution of these three races as given by Bishop (1943, p. 189) in his "Handbook of Salamanders" with the pattern that has resulted from the studies reported herein. The differences between these two distributional pictures are due, in large part, to the recent availability of new material.

These specimens are from a variety of sources, and I am deeply indebted to the following persons for making their personal collections, or collections under their supervision, available to me for the purposes of this study: Dr. E. R. Dunn, Academy of Natural Sciences of Philadelphia; Charles M. Bogert, American Museum of Natural History; Dr. Sherman C. Bishop; M. Graham Netting and Dr. Grace Orton, Carnegie Museum; Clifford H. Pope, Chicago Natural History Museum; Ralph Dury, Cincinnati Museum of Natural History; Roger Conant; Miss Fanny A. Cook, Mississippi State Game and Fish Commission; Arthur Loveridge, Museum of Comparative Zoology; Dr. Wilfred T. Neill, Ross Allen's Reptile Institute; Dr. Doris M. Cochran, United

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States National Museum; and Drs. Norman Hartweg and Charles F. Walker, University of Michigan Museum of Zoology. I have also studied material deposited in the collections of the departments of biology at the University of Rochester and the University of Florida. Counties from which I have seen specimens are indicated by the symbols on Figure 2. This map summarizes the raw data upon which the following remarks are partly based.

Each symbol represents anywhere from a single individual to a number of series of specimens collected in the county indicated. Each series was considered a sample of the population and, consequently, each symbol is an estimated characterization of the county's population rather than a record of the individual variations of the specimens observed. In a very few instances, literature records were included on this map when they represented counties from the interior of the range of a race. The maps are the work of Miss Esther Coogle, staff artist and research assistant in the department of biology, University of Florida.

Desmognathus f. fuscus can be distinguished most readily from the other two races by its possession of a relatively uniformly and lightly pigmented venter. In 1940, Carr listed this form as occurring in the Appalachian River Valley (p. 50-51) in western Florida. Bishop (1943) did not include Florida in his distribution of *fuscus* presumably because of the apparent isolation and the unsupported nature of the alleged Florida material. There are now many specimens of *fuscus* in the collections of the department of biology of the University of Florida, and there is no doubt that this race occurs in the Appalachian region. In March of 1948, Messrs. Cooper, Kilby, McConkey, and Reid and myself secured many specimens of *fuscus* in the Appalachian River Valley and also collected typical *auriculatus* (*auct.*) to the east and west of this area. Additional recent collections are at hand.

It seemed logical to infer that since *fuscus* had been able to migrate southward in the Flint-Appalachicola it might have been able to do so in other Gulf Coast river systems. To investigate this possibility, collections of *Desmognathus* were sought from the Alabama and Mobile River Valleys and a few samples were studied that had been taken near Mobile, Alabama. *Desmognathus f. fuscus*

UMMZ 97375) was represented in some of this material. The indication is, therefore, that *fuscus* has invaded the Gulf Coast along those rivers which have their headwaters in upland *fuscus* territory. The Alabama, Mobile, and Appalachian seem to be the major rivers of this type, and all appear to have *fuscus* inhabitants.

Desmognathus f. brimleyorum is a form restricted to the Ozarks, as mapped by Bishop, and *auriculatus* is pictured by him as a race of the lower Gulf Coastal Plain and the Atlantic Coastal Plain. There has been considerable

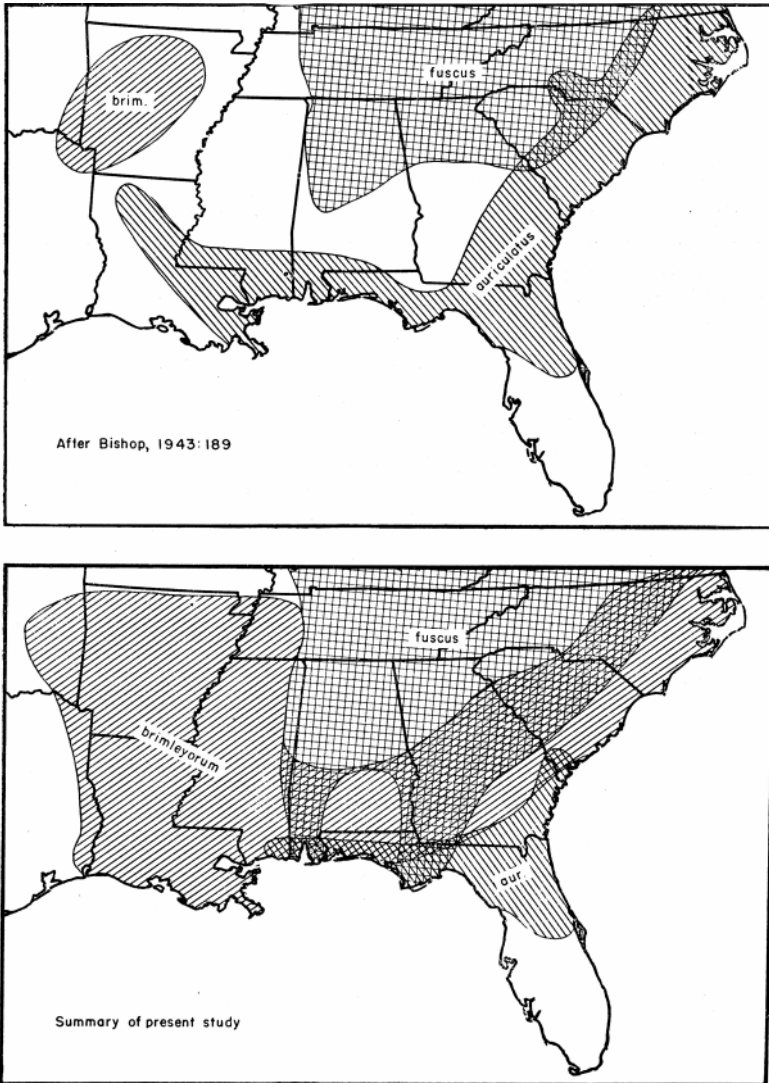


Figure 1. Distribution of the races of *Desmognathus fuscus*. The upper map shows the distributional picture taken from the latest summary of the genus and the lower map shows, in a general fashion, the results of the present study. The major changes are the descent of *fuscus* along the Gulf Coast river valleys; the severe restriction of the range of *auriculatus*; and the considerable extension of the range of *brimleyorum*. The wide bands of overlapping textures in the lower map indicate, for the most part, an interdigitation of races rather than extensive intergradation.

difficulty in accurately delimiting the two races. Material from Louisiana has caused problems. Dunn (1926, p. 101, 105) apparently considered intergradation to be demonstrated in the Gulf Coastal Plain. He pointed out that individuals of *auriculatus* (auct.) from the Mississippi Valley are lighter in appearance than those from Georgia and Florida. Bishop had a hiatus between the animals he recognized as western *auriculatus* and *brimleyorum* and was therefore unable to observe such intergradation if it existed. The most outstanding, and most recent, example of the difficulty in identifying these two races, on the basis of present distribution and character analysis, is demonstrated by Sanders and Smith (1949, p. 28). These workers reported on two specimens collected in Votaw, Hardin County, Texas, assigning one to *brimleyorum* and the other to *auriculatus*. Of the latter, they suggested that it represented the first example of the race collected in Texas. Sanders and Smith went to a considerable amount of trouble to justify the occurrence of two races in one county. They offered several suggestions (including the possibility of elevating the two forms to specific rank), none of which, however, was concerned with the proper identification of the specimen they designated as *auriculatus*.

A further question is thrown on the present distributional picture by the fact that, except for *Plethodon ouchitae*, there is no other non-cave plethodontid restricted to the Ozarks. It is worthwhile investigating, therefore, whether *brimleyorum* is actually an Ozark endemic or whether it has a wider distribution. The Mississippi specimens made available by Miss Cook have helped tremendously in this phase of the study.

A first consideration involves likely character differences between *auriculatus* (auct.) and *brimleyorum* (auct.). Since preservation so radically affects color and proportions, I have made use of several samples of living material. I have been fortunate in obtaining live specimens from several localities in the Ozarks through the generosity of Dr. Joe A. Tihen, from the vicinity of New Orleans through the generosity of Dr. Fred Cagle, and from the vicinity of Gainesville, Florida, through the kindness of students and colleagues at the University of Florida. It is readily apparent in living material that two quite different forms are present--one is a very dark brown to jet black animal (hereafter called black) and the other is brown or light gray (hereafter called brown).

In order to evaluate the genetic basis for these color differences, a pair of relatively crude experiments was executed. A collection of black salamanders from Gainesville was divided into two groups. One group of specimens was placed in a situation so that it received continual light twenty-four hours a day for ten days. The other was put in a similar situation except that the

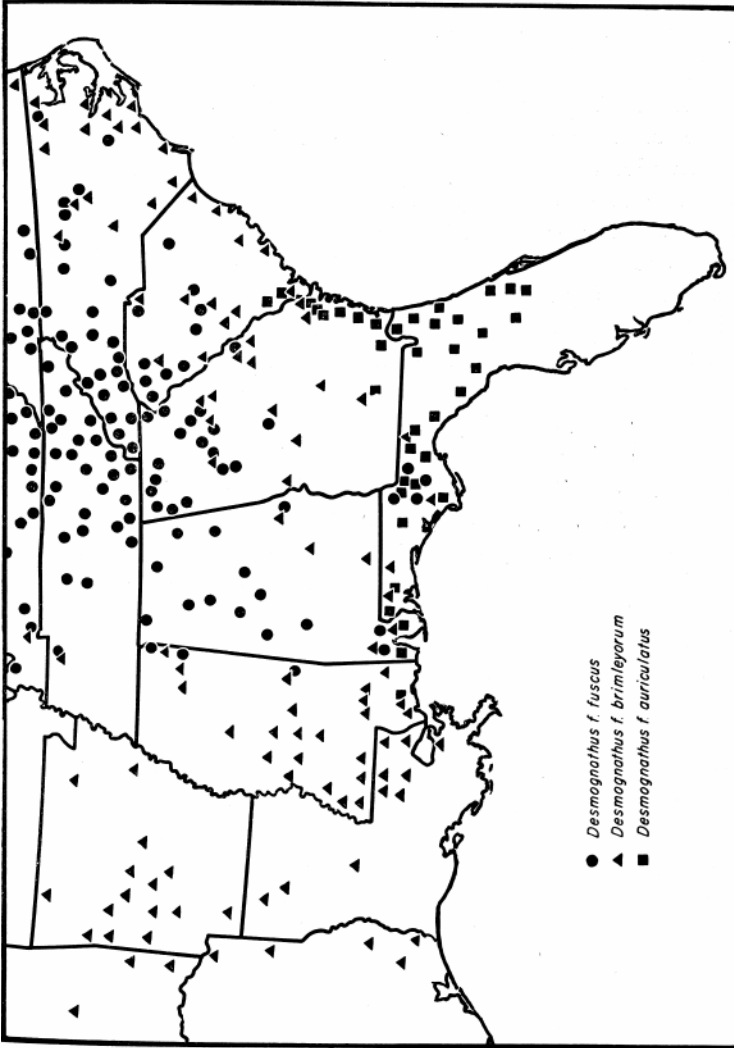


Figure 2. Distribution of the races of *Desmognathus fuscus*. Each symbol represents an estimate of the racial identity of one or more series of specimens from a county. When two different collections from a county indicated the presence of two different races (in Liberty County, Florida, e.g., *fuscus* in the Appalachicola River Valley and *auriculatus* in the surrounding area), both symbols were used. Samples of apparently intergrading populations were assigned to the race the most nearly resembled. A very few symbols indicate literature records.

specimens were kept in complete darkness for the same period. At the same time, a parallel experiment was done with a small series of brown salamanders from New Orleans. At the end of the experimental period, the four groups of salamanders were preserved. The black salamanders which had been continuously illuminated were lighter in color than the blacks which had been kept in the dark. Similar results were obtained with the brown salamanders from New Orleans. However, and this is the important point, the "light" black Gainesville salamanders were still distinguishable from, and darker than, the "dark" brown New Orleans *desmognaths*. Obviously, environmental conditions can exert a great effect on the intensity of color of these animals. Yet, at least under the conditions of this experiment, there is a residual amount of color difference that is presumably due to the difference in genetic make-up. So, although there is a good deal of variability in color due to extraneous factors (i.e., other than genetic), it does appear that the general black-brown difference between New Orleans and Gainesville *desmognaths* is a reflection of a fundamental genetic difference.

It has been suggested (Knepton, 1950) that the difference between brown salamanders and black salamanders in *Desmognathus* is due to the number of melanin particles in the dermal melanophores. Knepton believes that brown salamanders have fewer melanin particles per melanophore than black salamanders. Although Knepton was working with extreme individuals from the Gainesville population, it does seem probable that the difference described may actually be the physical basis for the color difference between normal Gainesville and normal New Orleans *desmognaths*.

It now remains to determine the geographic distribution of the black and brown forms. Looking through collections of preserved material, it is relatively easy to pick out jet black specimens in contra-distinction to grays and browns. (This sorting process has been simplified by reference to the preserved experimental animals mentioned above.) The blacks seem to be limited to the northern half of peninsular Florida, southern Georgia, the southern tip of South Carolina, western Florida, and extreme southern Alabama and Mississippi. This area is one in which the river bottom soils are black (Leon-Bladen as described in the *Agricultural Yearbook*, 1938, p. 1113-5). It also includes the type locality (Riceborough, Liberty County, Georgia) of *auriculatus*. It would seem, then, that the black form, *auriculatus*, should be considered as restricted to the area just described, and it is so pictured in Figure 1.

The brown form is the one that occurs at Hot Springs, Arkansas, which is the type locality of *brimleyorum*. Available specimens of this brown race indicate a continuous distribution in the Mississippi River Valley. *Desmogna-*

thus *f. brimleyorum* is not, then, an upland Ozark endemic, but is to be regarded as a widespread Coastal Plain form that enters the Ozarks by means of river valleys. Apparently *brimleyorum* has a much wider distribution than *auriculatus* and is to be found in both the Atlantic and Gulf Coastal Plains as indicated in Figure 1.

Just as *fuscus* apparently travels downstream to invade the territory of *brimleyorum* and *auriculatus* in the Gulf Coast, so does *brimleyorum* appear to move upstream in *fuscus* territory along the Atlantic Coast. The wide band of overlapping textures covering the Fall Line in Figure 1 indicates interdigitation of the two races rather than extensive intergradation.

A feature worth mentioning is the presence of unusually large individuals of *brimleyorum* in the Ozarks which might be considered to be evidence for the restriction of the name as formerly allocated. Such giant specimens, however, crop up in the range of *fuscus* itself, being known from several counties in eastern Kentucky. Intergradation between *fuscus* and *brimleyorum* (as herein defined) in the Carolinas has been suggested by Bishop (1943, p. 189). In a recent series (D.B.U.F. 2669) of desmognaths collected in the Appalachianicola River Valley area (Torreya State Park) by Messrs. Beecher, Cooper, Hellman, and McConkey, students at the University of Florida, are specimens that could readily be allocated to *fuscus* or *auriculatus*. Intermediate specimens were also present in the series. This is taken to be evidence for intergradation between *fuscus* and *auriculatus* in an area where the two races meet in the flood plain of the Appalachianicola River.

One of the obvious conclusions one can derive from this work is a definition of areas in which further study would produce profitable results. In territorial terms, these areas would be indicated by the overlapping of map textures in Figure 1. For example, a detailed study of living desmognaths from western Florida, with special notice of their ecological relationships, would doubtless be of tremendous value in further clarifying the racial relationships among these salamanders.

A painstaking examination of material from all parts of the range will certainly disclose other well-marked races of *fuscus*. There may well be a grayish form in Louisiana and Mississippi; the giant specimens from Arkansas and Kentucky are also suggestive.

Our knowledge about the relationships of the races of *Desmognathus fuscus* may be summed up with the following words. It would seem that an upland brownish salamander (with a well-marked dorsum and a clear venter), much like present-day *fuscus*, was the progenitor of a coastal plain brown race, much like present-day *brimleyorum*. In evolving from *fuscus* to *brimleyorum* the changes involved were primarily a fading of the dorsal pattern and an in-

crease in the amount of ventral pigmentation. Arising in place on black soils from a brown *brimleyorum*-like ancestor was a black race, *auriculatus*, similar in most respects to *brimleyorum* except for an increase in the number of melanin particles in the dermal melanophores.

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